The tarsal sensory system
of *Amblyomma variegatum* Fabricius
(Ixodidae, Metastriata)

III. Mapping of sensory hairs and evolution of the relative importance of sensory modalities during post-embryonic development.

by

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With 5 Tables

ABSTRACT

The distribution of the 12 types of sensory hairs occurring on the front tarsi of *A. variegatum* are compared among larvae, nymphs, and adults. The evolution of the tarsal sensory system during the post-embryonic development of the tick is characterized by the increase of sensilla of all sense modalities from the larval to the nymphal stage, while, from nymphs to adults, the increase concerns predominantly tactile and gustatory sensory hairs. No difference is observed between males and females.

INTRODUCTION

Amblyomma variegatum larvae, nymphs, and adults possess 12 structurally different types of sensory hairs on their first pair of tarsi (HESS & VLIMANT 1982, 1983). These sensilla are classified according to the system proposed for insects by ALTNER (1977), distinguishing between no pore (np), terminal pore (tp), wall pore single-walled (wp-sw), and wall pore double-walled (wp-dw) sensilla (Table 1).

The first tarsi play a predominant role in host detection and host predilection site seeking, as ticks use their first legs in the same manner as insects use their antennae.

The comparison of the maps of distribution among the 3 instars of a tick species demonstrates the evolution of the tarsal sensory system during the development of a species and reflects the relative importance of stimulus modalities. Also interspecific comparisons of the number and distribution of the types of sensilla and of the number of associated sensory units could be of use to explain behavioral and ecological differences as well as the evolution of the host-parasite system.

MATERIAL AND METHODS

The microanatomy and distribution of the sensory hairs of all instars have been studied by transmission- and scanning electron microscopy (HESS & VLIMANT 1982, 1983). To designate the sensory hairs and their position a code composed of one or two letters, a Roman and an Arabic numeral, is used (e.g. dI2). The letters indicate the face of the tarsus (d for dorsal, v for ventral, la for lateral anterior, lp for lateral posterior), Roman numerals indicate the groups of sensilla (numbering from distal to proximal; exception: the group of sensilla located in the capsule of Haller's organ is designated by the initial C), and Arabic numerals are used to number the sensilla within a group. This code has been presented in detail in previous papers (HESS & VLI-MANT 1982, 1983).

RESULTS AND DISCUSSION

I. EVOLUTION OF THE GROUPS OF SENSILLA DURING DEVELOPMENT

A. variegatum, like all other ticks species, possesses relatively few sensory hairs. This allows for easy mapping. The number and distribution of the sensilla is extremely constant from one specimen to the other. Individual differences (± 1 hair) occur only in the most proximal groups (d VI, la II, lp II, v V), especially in adults.

A characteristic evolution of the number and innervation of sensory hairs occurs during the post-embryonic development of the tick, but there is no difference in the number and innervation of sensilla between males and females. Tables 2-4 show the maps of the four faces of larval, nymphal, and adult tarsi I, indicating the position of the groups of sensory hairs and the location of the different sensilla within the groups. Table 5 shows the evolution of the total number of setae and the associated sensory cells independent of their location, in the three instars. For the following comparisons Tables 2-4 should be consulted.

Comparison of the dorsal faces

The larval group d I (commonly called the "distal group") seems to be composed of two sensilla when observed with the scanning electron microscope, comprising an anterior np/C, and a posterior wp-sw/A hair. In nymphs and adults we find two sensilla of the same types in this location, but in an inversed position. However, the larval np/C sensillum does not belong into the group d I, but represents the lateral sensillum la I 1, situated somewhat dorsally in the first instar. Thus the larval group d I possesses only a single sensillum, which is of the wp-sw/A type. In nymphs, the np/C

sensillum la I 1 takes a clear lateral position and a second np/C hair (d I 2) appears in the group d I, posterior to the wp-sw/A sensillum, i.e. there is no inversion of the position of sensilla from larva to nymph. This situation remains unchanged in adults. This manner of development of the group d I is much clearer in *Boophilus microplus* and *Dermacentor marginatus* where the larval np/C sensillum is situated on the lateral anterior face from the beginning.

The two np/C hairs discussed above are important for host seeking (this type seems to be restricted to the first tarsus). They contain (besides 2 mechanoreceptors) a warm and a cold unit as demonstrated electrophysiologically in adults (Hess & Loftus in preparation). The innervation of the sensillum la I 1 evolves in an interesting manner. In larvae and nymphs, the shaft is innervated only by a single sensory unit, but in adults two sensory cells are present. Thus, the la I 1 hair lacks either the warm cell or the cold cell in the first two instars. This demonstrates that the innervation of a sensillum can evolve during the development of the tick. It would be important to know if the cold or the warm cell develops first and if one of these cells is phylogenetically older than the other. The shaft of the second np/C sensillum d I 1, which appears first in nymphs, is innervated by two units from the beginning.

The number and distribution of sensilla in the group d II (anterior pit of Haller's organ) remains the same in all instars. Notice, that the types np/D, np/E, and wp-dw/C are restricted to this group. Sensillum d II 1 (wp-sw/A type) which is innervated by a single set of 5 neurons in larvae, possesses 3 sets of 5, 5, and 4 neurons respectively in nymphs and adults, each group being surrounded by a sheath of its own. This triple innervation in nymphs and adults is explained evolutionarily by the fusion of originally 3 independant wp-sw/A sensilla in the anterior pit of Haller's organ. This hypothesis is partially confirmed by other species such as *A. americanum* and some Haemaphysalinae, where the corresponding sensillum d II 1 of larvae has a single group of 5 sensory cells while nymphs and adults possess 2 setae of this type, one with a group of 5 sensory units, the other with 2 groups of 5 and 4 neurons. The supposed primitive case with 3 independent wp-sw/A sensilla in the group d II has yet to be found.

Group C (Capsule of Haller's organ) is composed of wp-sw/B sensilla which are restricted to this group. Their number increases from 4 in larvae to 7 in nymphs and adults.

Group d III which is composed of a np/A and a wp-dw/B sensillum remains unchanged in all instars.

The larval group d IV has 2 wp-dw/A hairs innervated by 2 sensory cells each. In nymphs, a second set of 2 wp-dw/A sensilla is added, but these setae are innervated by only one neuron each. Wp-dw/A sensilla are only found in group d IV.

Group d V with 2 tp/A sensilla appears first in nymphs and remains unchanged in adults.

In the group d VI, the number of tactile np/B bristles increases from instar to instar, and in adults, a tp/A sensillum appears.

Comparison of the ventral faces

The larval and nymphal group v I are equipped with a pair of tp/B (restricted to this group) and a pair of np/A sensilla while adults also possess a pair of tp/A sensilla.

Group v II is lacking in larvae but appears with 2 np/A hairs in nymphs, remaining unchanged in adults.

In the group v III, both lateral sensilla are wp-dw/B hairs. The two middle sensilla (v III 3 and v III 4) are of the np/A type in larvae. In nymphs, the posterior one

(v III 4) becomes of the tp/A type, and in adults, the anterior one (v III 3) also transforms into a tp/A sensillum. The question is whether the group of cells associated with the original np/A sensilla v III 3 and v III 4 is able to transform into tp/A specific cells or the whole np/A set is replaced by tp/A specific cells during development.

Group v IV comprising 2 tp/A sensilla appears only in adults.

The larval group v V has a pair of np/A sensilla, to which several other np/A and 1 or 2 tp/A hairs are added in nymphs and adults.

Comparison of the lateral anterior faces

The lateral anterior faces bear a single np/C (with 1 sensory unit in larvae and nymphs with 2 sensory units in adults), a single wp-dw/B sensillum, as well as np/B sensilla. The number of the latter increases from instar to instar.

Comparison of the lateral posterior faces

The lateral posterior faces bear a single tp/A sensillum and np/B sensilla, the number of which increases from instar to instar. The field lp I is not occupied in *A. variegatum*.

II. EVOLUTION OF THE TOTAL NUMBER OF THE 12 TYPES OF SENSILLA AND RELATED SENSORY CELLS DURING DEVELOPMENT

The comparison of the numbers of the different types of sensory hairs among the three developmental stages of the tick informs us about the relative importance of the sensory modalities in each instar provided we are informed about the function of the different types of sensilla (Table 1). More detailed information is produced when we compare not only the number of setae but the number of sensory cells per type, as the degree of innervation varies among the different types of sensilla. Furthermore, in sensilla chaetica we should consider separately the machanosensory units (MSU) which possess tubular bodies, and the shaft innervating units (SIU) representing other than tactile senses (Table 5).

Comparison between larval and nymphal tarsus I

The number of wp-sw/A sensilla remains equal in both instars, but the number of SIU increases from 10 to 19 (9 "new" SIU in nymphal d II 1). In wp-sw/B, wp-dw/A, and tp/A sensilla, the number of hairs and the number of SIU grows from larvae to nymphs. Thus, olfactory (wp-sensilla) and gustatory (tp-sensilla) chemoreception becomes apparently more important for nymphs. However, it has to be mentioned that these olfactory— and gustatory chemoreceptors may also contain thermo— and hygrosensitive SIU. There is indeed evidence that tp/A sensilla can contain thermosensitive cells (WALADDE *et al.* 1981). Improvement of thermoreception in nymphs is also achieved by the increase of np/C thermosensitive SIU.

The increase of monomodal mechanosensory sensilla (tactile bristles) occurs predominantly in the proximal part of the tarsus which becomes equipped with np/A sensilla on the ventral face and np/B sensilla on the other 3 faces.

No increase of sensory units occurs in the types wp-dw/B, wp-dw/C, tp/B, np/D, and np/E.

Comparison between nymphal and adult tarsus I

The most striking evolution concerns the strong increase of gustatory tp/A hairs in adults, while the number of olfactory sensilla and SIU remains at the nymphal level. This could mean that taste plays an important role in the sexual behavior of this tick. Thermoreception is completed in adults by the increase of thermosensitive units associated with tp/A sensilla and by the addition of an antagonistic thermoreceptor cell to the np/C sensillum la I 1.

The tactile sense becomes developed by numerous new np/A and np/B sensilla which occupy the new proximal surface. The number and innervation of all other types of sensilla do not change from nymphs to adults.

Additional remarks

i) The numbers of sensory hairs and sensory cells given above refer to *one* tarsus I. Thus, a tick possesses twice as many of these cells and sensilla.

ii) Tp/A sensilla are distributed over the segments of all legs, and 4 tp/A-like sensory hairs (16 SIU) occur also on the palps together with 6 tp/B setae (42-66 SIU) in nymphs and adults (larvae lack 2 setae with 10 SIU). Thus, to estimate the whole gustatory potential of the tick, all these SIU have to be added to those occurring on the first tarsi.

III. COMPARISONS WITH OTHER SPECIES

1. The basic pattern of distribution of the different types of sensory hairs in Metastriata roughly seems to be that of *A. variegatum*.

2. In the genus *Ixodes* (Prostriata), the pattern observed in *A. variegatum* is easily recognized in spite of important deviations from the Metastriata map (THONNEY in preparation).

3. Argasids show a simplified pattern which is, however, comparable to the Metastriata map (Hess & Thüring, in preparation).

4. In our opinion, the comparison of the maps of tarsal sensilla is a method to elucidate the evolution of tick species as well as the evolution of the host-parasite relationship. There is, however, one *conditio sine qua non*: The comparisons have to be based on exhaustive studies made by scanning and transmission electron microscopy and they should be supported by electrophysiological research.

type	symbols used in tables II, III, IV	functions					authors
		olfactory	gustatory	thermo-sensitive	hygro-sensitive	mechano-sensitive	
wp-sw/A	⊙_A	+	-	?	?	-	1) 3) 4) 5) 8)
wp-sw/B	⊙_B	+	-	?	?	-	1) 7)
wp-dw/A	∅_A	+	-	?	?	-	1) 3)
wp-dw/B	∅_B	?	-	?	?	*	1)
wp-dw/C	∅_C	+	-	?	?	-	1) 3)
tp/A	⊙_A	-	+	+	?	*	1) 2) 9)
tp/B	⊙_B	-	+	?	?	*	1) 2)
np/A	○_A	-	-	-	-	*	1)
np/B	○_B	-	-	-	-	*	1)
np/C	○_C	-	-	+	-	*	1) 6)
np/D	○_D	-	-	?	?	-	1)
np/E	○_E	-	-	?	?	-	1)

TABLE 1.

The 12 types of tarsal sensory hairs and their demonstrated or presumed functions.

+: electrophysiologically demonstrated in ixodid ticks; *: evident from structure (Thurm 1964); ?: possible from structure, or electrophysically demonstrated in comparable sensilla of insects; -: excluded. Authors: 1) Altner & Prillinger 1980; 2) Balashov et. al. 1976; 3) Haggart & Davis 1980; 4) Haggart & Davis 1981; 5) Hess & Vlimant 1982; 6) Hess & Loftus, in preparation; 7) Sinitzina 1974; 8) Thonney, in preparation; 9) Waladde et al. 1981.

dorsal	lateral posterior	ventral	lateral anterior
		v I 2,1... O_B O_B	
		4,3...	
		6,5... O_A O_A	distal
d I 1...... Θ_A	lp I	v II	la I 1... O_C
d II 1..... Θ_A			
2,3,4. O_E O_E O_D			
5,6 $\emptyset_C$ $\emptyset_C$			
pseudosegmental groove			
C 1,2...... Θ_B Θ_B		v III	
3,4...... Θ_B Θ_B	lp II 1.. O_A	4,3,2,1... $\emptyset_B$ O_A O_A $\emptyset_B$	la II 1.. $\emptyset_B$
d III 1,2.. O_A $\emptyset_B$		v IV	
	2.. O_B		2.. O_B
d IV 1,2... $\emptyset_A$ $\emptyset_A$		v V 2,1... O_A O_A	
d V			
d VI 1,2... O_B O_B			proximal

TABLE 2.

Map of the four faces of the right larval tarsus I indicating the position of the different types of sensory hairs (right of each column) and their corresponding code (left of each column). For explanation of the symbols refer to table I.

dorsal	lateral posterior	ventral	lateral anterior	
		v I 2,1... O_B O_B 4,3... 6,5... O_A O_A		distal
d I 1,2.... Θ_A O_C	lp I	v II 2,1.. O_A O_A	la I 1... O_C	
d II 1..... Θ_A r 2,3,4. O_E O_E O_D 5,6... $\emptyset_C$ $\emptyset_C$				
pseudosegmental groove........	....	....	....	
C 1,2...... Θ_B Θ_B 3,4,5.... Θ_B Θ_B Θ_B 6,7...... Θ_B Θ_B	lp II 1.. O_A	v III 4,3,2,1... $\emptyset_B$ O_A O_A $\emptyset_B$	la II 1.. $\emptyset_B$	
d III 1,2.. O_A $\emptyset_B$		v IV		
d IV 1,2... $\emptyset_A$ $\emptyset_A$ 3,4... $\emptyset_A$ $\emptyset_A$	2.. O_B	v V 1..... O_A	2.. O_B	
d V 1,2.... O_A O_A		2..... O_A		
d VI 1..... O_B		3..... O_A		
2..... O_B	3.. O_B	4..... O_A	3.. O_B	proximal
3..... O_B		5..... O_A		

TABLE 3.

Map of the four faces of the right nymphal tarsus I indicating the position of the different types of sensory hairs (right of each column) and their corresponding code (left of each column). For explanation of the symbols refer to table 1.

dorsal	lateral posterior	ventral	lateral anterior	
		v I 2,1... O_B O_B		distal
		4,3... O_A O_A		
		6,5... O_A O_A		
d I 1,2.... Θ_A O_C	lp I	v II 2,1.. O_A O_A	la I 1... O_C	
d II 1..... Θ_A				
2,3,4. O_E O_E O_D				
5,6... $\emptyset_C$ $\emptyset_C$				
pseudosegmental groove				
C 1,2...... Θ_B Θ_B		v III		
3,4,5.... Θ_B Θ_B Θ_B	lp II 1.. O_A	4,3,2,1... $\emptyset_B$ O_A O_A $\emptyset_B$	la II 1.. $\emptyset_B$	
6,7...... Θ_B Θ_B				
d III 1,2.. O_A $\emptyset_B$		v IV 2,1.. O_A O_A		
d IV 1,2... $\emptyset_A$ $\emptyset_A$	2.. O_B	v V 1..... O_A	2.. O_B	
3,4... $\emptyset_A$ $\emptyset_A$		2..... O_A		
		3..... O_A		
d V 1,2.... O_A O_A		4..... O_A		
		5..... O_A		
d VI 1..... O_A	3.. O_B	6..... O_A	3.. O_B	
2..... O_B	4.. O_B	7..... O_A	4.. O_B	
3..... O_B	5.. O_B	8..... O_A	5.. O_B	
4..... O_B	6.. O_B	9..... O_A	6.. O_B	
5..... O_B	7.. O_B	10.... O_A	7.. O_B	proximal
6..... O_B	8.. O_B		8.. O_B	
7..... O_B	9.. O_B			
8..... O_B				
9..... O_B				

TABLE 4.

Map of the four faces of the right adult tarsus I indicating the position of the different types of sensory hairs (right of each column) and their corresponding code (left of each column). For explanation of the symbols refer to table I.

types of SH	LARVA			NYMPH					ADULT				
	nbr SH	totnbr SIU	totnbr MSU	nbr SH	totnbr SIU	incr SIU L→N	totnbr MSU	incr MSU L→N	nbr SH	totnbr SIU	incr SIU N→A	totnbr MSU	incr MSU N→A
wp-sw/A	2	10	0	2	19	9	0	0	2	19	0	0	0
wp-sw/B	4	12-20¹⁾	0	7	21-35	9-15	0	0	7	21-35	0	0	0
wp-dw/A	2	4	0	4	6	2	0	0	4	6	0	0	0
wp-dw/B	4	16-28	8	4	16-28	0	8	0	4	16-28	0	8	0
wp-dw/C	2	6	0	2	6	0	0	0	2	6	0	0	0
tp/A	2	6-12	4	6	18-36	12-24	12	8	13	39-78	21-42	26	14
tp/B	2	8	4	2	8	0	4	0	2	8	0	4	0
np/A	6	0	12	9	0	0	18	6	12	0	0	24	6
np/B	4	0	8	7	0	0	14	6	23	0	0	46	32
np/C	1	1	2	2	3	2	4	2	2	4	1	4	0
np/D	1	3	0	1	3	0	0	0	1	3	0	0	0
np/E	2	6	0	2	6	0	0	0	2	6	0	0	0
totals	32	72-98	38	48	106-150	34-52	60	22	74	128-193	22-43	112	52

TABLE 5.

Comparison of the number of sensory hairs of the 12 different types and the related sensory cells on the larval, nymphal, and adult tarsus I. ¹) in sensilla with variable innervation, the minimum and maximum possible numbers of neurons are indicated. Abbreviations: totnbr: total number; incr: increase; SH: sensory hair; SIU: shaft innervating sensory units; MSU: mechanosensory units; L: larva; N: nymph; A: adult.

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